

# Growth Rates and Growth Periodicity of Tree Roots

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I. Introduction . . . . .	181
II. The Root System and Growth Rates of Tree Roots . . . . .	182
A. The Root System . . . . .	182
B. Periodicity of Root Growth . . . . .	194
C. Root Growth and Environmental Conditions . . . . .	202
D. Practical Considerations . . . . .	224
References . . . . .	226

## I. Introduction

For a long time the root system was regarded only as an auxiliary organ of the plant providing mechanical fastening in the soil and absorbing water and mineral salts. These functions are indeed important, but it should be kept in mind that roots are highly specialized organs in which numerous syntheses are performed (Mothes, 1956). Water uptake and mineral absorption, according to modern concepts, are closely related to metabolic activity and growth of roots. From many practical experiences it is well known that vigorous root growth is necessary for good shoot growth and that disturbances in root growth impair shoot growth.

In spite of this, relatively little is known about growth behavior of roots. This is mainly because of difficulties arising from the methods used. Many failures in cultural techniques result from ignorance of the normal course of root growth and of the influences of environmental conditions upon it. Numerous questions are still almost uninvestigated,—for example, the correlative reciprocal effects between root and shoot systems, the influence of environmental factors on the intensity and course of root growth, and specific optimum values for the different tree species.

At present it is difficult to draw general conclusions from the statements in the literature because environmental conditions and research techniques have varied widely and often have been only inadequately described. As is described in detail in the last part of this article, practical conclusions could be drawn from better knowledge about root growth. The possibilities in this field will be much expanded with increasing knowledge on the specific requirements of various tree species for good root growth. Optimal conditions for vigorous root growth are as important for high productivity as are good conditions for shoot growth. Although this has often been said, little is really known in detail. The physiology and ecology of root growth are still a neglected segment of plant physiology.

## II. The Root System and Growth Rates of Tree Roots

### A. The Root System

#### 1. THE GROSS ROOT SYSTEM

Many investigations on the structure of the root system of trees have been performed during recent decades to get information on the specific peculiarities of root morphology and on the extent of utilization of the soil volume by trees growing on different sites. Valuable knowledge was obtained by such static surveys on trees of different ages and on different sites. By investigating root arrangement and distribution in the soil, practical conclusions were drawn for silviculture and horticulture. Only some of the most important papers on this subject can be cited here.

The root system of *Fagus silvatica* was studied by Zielaskowski (1898), Krauss and co-workers (1934, 1935, 1939), Bonnemann (1939), Krahel-Urban (1951), Petsch (1955), and Hausdörfer (1959). That of *Pinus silvestris* was investigated by Tolsky (1904), Aaltonen (1920), Kokkonen (1923), Liese (1926), Hilf (1927), Laitakari (1929), Wagenhoff (1938), Simanjuk (1950), Kalela (1950), Rachtejenko (1952), Yeatman (1955), and Hausdörfer (1959). Concerning the root system of *Pseudotsuga taxifolia* Britt. there are the papers of Groth (1927), Wagenknecht (1958), and McMinn (1963); for *Picea abies* there are the reports of Vater (1927), Wagenknecht and Belitz (1959), Wiedemann (1927), Krauss and co-workers (1934, 1935, 1939), Kern *et al.* (1961), and Melzer (1962b). The root system of *Quercus borealis* var. *maxima* was studied by Lemke (1955). In addition, information on several other tree species, mostly North American, may be found in the papers of Holch

(1931), Biswell (1934), Coile (1937), Scully (1942), Joachim (1953), Kreutzer (1961), Dchjen (1962), and Lyford and Wilson (1964). Kreutzer (1961) and Heikurainen (1964) have reported on root development of some tree species under the influence of soil water conditions which were changing as a result of amelioration measures.

The results show that it is difficult to establish general, intraspecific rules of root development because site and soil conditions modify root formation to such a degree that peculiarities of the species are partly or entirely obscured (Wittich, 1947; Wagenknecht, 1955). In spite of this limitation available knowledge of root development has allowed some conclusions to be drawn about the practical utilization of trees in silviculture and horticulture, conclusions which are of special importance for soils with different layers or with high resistance to the penetration of roots (Kvarazhelia, 1931; Wagenknecht, 1955; Kreutzer, 1961).

In many cases structure and reactivity of the root system are of decisive significance in determining site latitude and site tolerance of a tree species. The early development of a plant is in especially close correlation with its ecology, because it is often decided in the seedling stage whether a species is able to colonize a particular site. Quick reaching of deeper soil layers which are not in danger of drying out, and a sufficient ability to compete with roots of other species, are decisive factors in natural and artificial reproduction. Tree root systems consist of various types of morphologically and functionally different roots. The most generally used nomenclature for the different parts of the root system is given in a schematic way in Fig. 1.

Some tree species have a tendency to form taproots. This is most obvious in seedlings and is often found in species with large seeds rich in reserve foods, such as *Quercus*, *Carya*, *Castanea*, and *Juglans*. In these the taproots also serve as storage organs for the seedling. Taproots may sometimes be observed in other genera, notably *Pinus*. They are well suited for quickly reaching greater soil depths and are quickly and preponderantly developed during the juvenile phase at the expense of the storage material of the seeds, whereas the development of the shoots is at first rather slow and sometimes restricted to one or very few leaves, especially so in some desert plants (Kausch, 1959).

Taproots are able to reach low ground-water levels and secure the water supply of a tree even in dry areas. Such roots can grow down to considerable depths; for example, 18-year-old apple trees to 10 m (Wiggins, 1936); *Robinia* to 20 m (Schimper and Faber, 1935); *Prosopis* to 15 m; and *Tamarix* to as much as 30 m (Kausch, 1959). A strong horizontal

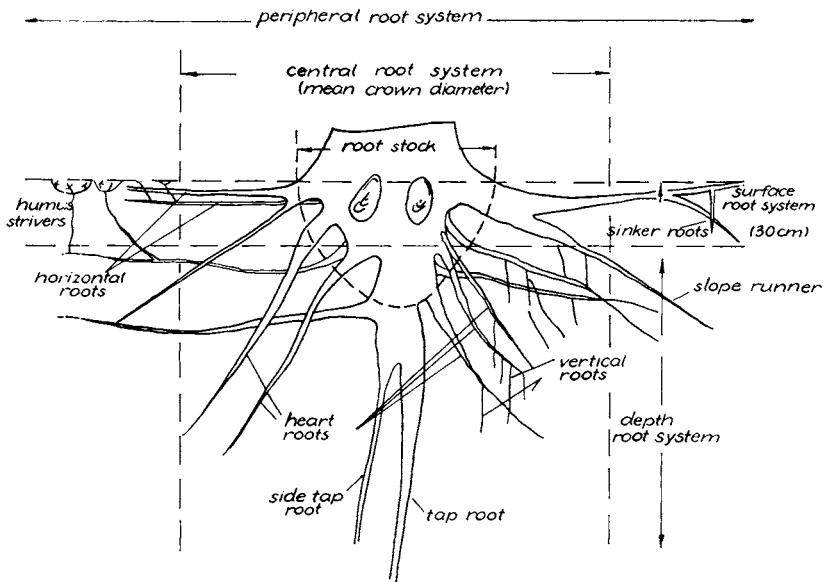


FIG. 1. Schematic representation of a root system with most used nomenclature (according to Melzer, 1962b). For diameter classes the classification of Grosskopf (1950) and Kreutzer (1961) is proposed (approximately equivalent English terms are given here): finest roots,  $< 0.5$  mm; fine roots,  $0.5 - 2$  mm; weak roots,  $2 - 5$  mm; firm roots,  $5 - 10$  mm; rough roots,  $10 - 20$  mm; strong roots,  $> 20$  mm. According to Grosskopf (1950), "fine root capacity" means root weight or length of roots from  $0.5$  to  $2$  mm per liter of soil; "finest root capacity" means roots  $< 0.5$  mm in diameter per liter soil.

root development may be observed on poor sites (such as sand dunes) where *Pinus*, *Betula*, and *Robinia* may form roots  $10$ ,  $20$ , or even  $40$  meters long, which often results in considerable root competition. Roots of *Acer rubrum* may also reach a length of  $25$  m (Lyford and Wilson, 1964).

A shallow, superficially expanded root system, which is typical of *Picea* species, is very effective in absorbing the ephemeral moisture after rains or melting snow, especially on shallow, rocky soils, which may be an ecological advantage in the mountains or in deserts. In the *Cactaceae* a superficial root system is combined with an astonishing ability for quick regeneration of root tips, which is a special mechanism of drought resistance (Kausch, 1955).

In orchard trees the horizontal expansion of the root system is normally one and a half to two times as large as the crown diameter (Kolesnikow,

1962b). In some cases it amounts to three to five times the crown radius (Kvarazhelia, 1931). This seems to be true also for other trees growing as solitaires, but the relations may be strongly modified by the environment. This should be noted in practical fertilization of older trees, in which the highest concentration of absorbing fine roots occurs at some distance from the trunk. It should also be kept in mind that there exist differences in root morphology, not only between tree species, but also between their provenances, which may be correlated with differences in growth performance. This was demonstrated in *Pinus silvestris* by Bibelriether (1964).

## 2. THE FINE ROOT SYSTEM

Investigations of the root system often concern only the gross root system. Although valuable conclusions may be drawn, it should be kept in mind that the quantity and activity of fine roots are primarily decisive for water and mineral salt supply of a tree. At present only a few investigations have been published in this field (e.g. Coile, 1937; Grosskopf, 1950; Grunert, 1955; Hausdörfer, 1959; Kern *et al.*, 1961; Buchholz and Neumann, 1964; Zöttl, 1964; see the latter for further literature).

Diameter analyses of roots of young plants show that the major part of the root system consists of fine roots. From Table I it may be seen that in the four tree species investigated in detail, although only 14 to 60% of the total root weight is represented by fine roots under 1 mm in diameter, these make up 86 to 99% of the total root length. The proportion of the total root surface represented by fine roots is, of course, much higher still. As may be seen from the investigations of Coile (1937) or Hausdörfer (1959) in soil profiles, these relations are similar in mature trees, although the weight relations may be different.

Root weight is a less suitable index than root length. Length is better correlated with surface development, a most important factor affecting physiological activity and exchange of substances (Grosskopf, 1950).

With increasing soil depth the proportion of fine roots increases. The different percentages which the single diameter classes contribute to total root weight and length in Table I show specific peculiarities in the root formation of the four tree species.

From our knowledge of root quantities, no direct conclusions about root activity can be drawn, although a loose correlation may be expected to exist. At present, detailed, comparable investigations are lacking. Surely the activity of mycorrhizae is very important. But this activity depends partly on the fungal species, which fact complicates the problem (Ritter and Lyr, 1965).

TABLE I  
ABSOLUTE AND RELATIVE AMOUNTS OF ROOTS OF DIFFERENT DIAMETER CLASSES IN ONE-YEAR-OLD  
ROOT SYSTEMS OF FOUR TREE SPECIES<sup>a</sup>  
(Data from Hoffmann, 1966c)

Tree species	Total		Diameter classes											
			<1 mm		1-2 mm		2-3 mm		3-4 mm		4-5 mm		>5 mm	
	Abs.	%	Abs.	%	Abs.	%	Abs.	%	Abs.	%	Abs.	%	Abs.	%
<i>Populus euramericana</i> "I 214"	w	43.9	100	11.6	26.4	4.2	9.6	4.5	10.2	4.1	9.3	3.2	7.3	16.3
	l	1567.0	100	1544	98.5	12.7	0.8	4.4	0.3	2.1	0.1	1.0	0.06	2.4
<i>Populus trichocarpa</i>	w	62.6	100	37.8	60.4	7.1	1.1	4.8	0.8	4.9	0.8	3.2	0.5	4.8
	l	384.7	100	364.2	94.6	13.9	3.6	3.1	0.8	1.6	0.4	1.3	0.3	0.6
<i>Robinia pseudoacacia</i>	w	58.5	100	9.5	16.2	5.9	10.0	8.8	15.0	7.0	12.0	8.8	15.0	18.5
	l	277.8	100	258.6	93.0	8.6	3.1	6.5	2.3	1.3	0.5	1.5	0.5	1.4
<i>Quercus borealis</i> var. <i>marima</i>	w	124.7	100	16.8	13.5	14.9	11.9	11.8	9.5	14.7	11.8	14.0	11.2	52.6
	l	182.4	100	156.0	85.7	15.8	8.7	4.0	2.2	2.5	1.4	1.4	0.8	2.7

<sup>a</sup> w = dry weight in grams; l = length in meters.

## 3. GROWTH RATES OF FINE ROOTS

Measuring and recording the static state of the root system may be of value in solving many questions. From a physiological point of view, however, the dynamic of root development is of greater importance. Because of unequal penetration of precipitation through soil fissures, old root tubes, and differently permeable soil areas, and because of the local un-

TABLE II  
MAXIMAL AND AVERAGE DAILY INCREMENT OF INDIVIDUAL TREE ROOTS  
AND MAXIMAL DEPTHS OF ROOT SYSTEMS AT END OF FIRST YEAR OF GROWTH<sup>a</sup>

Tree species	Increment (mm)		Maximal depth develop- ment in one year (cm)	Authority
	Maximal	Average		
<i>Picea abies</i> (L.) Karst.	8	—	32	Hoffmann (1966a)
<i>Pinus silvestris</i> L.	12	—	58	Hoffmann (1966a)
<i>Pinus taeda</i> L.	3-5	—	—	Barney (1951)
<i>Pinus taeda</i> L.	25	—	—	Reed (1939)
<i>Pinus echinata</i> Mill.	25	—	—	Reed (1939)
<i>Larix leptolepis</i> Gord.	10	6.1	42	Hoffmann (1966a)
<i>Pseudotsuga taxifolia</i> Britt.	16	4.7	54	Hoffmann (1966a)
<i>Quercus robur</i> L.	12	—	—	Hoffmann (1966a)
<i>Quercus petraea</i> Liebl.	15	—	—	Hoffmann (1966a)
<i>Quercus macrocarpa</i> Michx.	—	—	188 s	Holch (1931)
<i>Quercus rubra</i> L.	—	—	79 s	Holch (1931)
<i>Quercus borealis</i> var. <i>maxima</i> (Marsh.) Ashe	18	6.2	49	Hoffmann (1966a)
<i>Carya ovata</i> (Mill.) K. Koch	—	—	89 s	Holch (1931)
<i>Juglans nigra</i> L.	—	—	149 s	Holch (1931)
<i>Tilia americana</i> L.	—	—	40 s	Holch (1931)
<i>Malus</i> -hybrid	3	—	—	Rogers (1939)
<i>Malus</i> sp.	25	9.4	—	Rogers (1939)
<i>Acer saccharum</i> Marsh.	1	—	—	Morrow (1950)
<i>Betula pendula</i> Roth.	—	9-10	—	Vorobieva (1961)
<i>Betula pendula</i> Roth.	15	8.8	72	Hoffmann (1966a)
<i>Populus trichocarpa</i> Torr. & Gray	28	—	101 c	Hoffmann (1966a)
<i>Populus euramericana</i> "I 214"	50	20.0	140 c	Hoffmann (1966a)
<i>Robinia pseudoacacia</i> L.	56	15.2	210	Hoffmann (1966a)
Same, but shaded to 40% of full daylight	26	9.1	110	Hoffmann (1966a)

<sup>a</sup> s = seedling; c = cutting.

equal water uptake of roots, the soil is frequently very inhomogeneously wetted. Furthermore, the capillary water conduction of most soils is too low to equalize the differences quickly enough, so that with increasing drying out the water supply available to absorbing roots is essentially a stagnant one. New water and mineral salt sources must be found by active root growth, which under such circumstances is an important factor in ecological competition. A high rate of root increment means the penetration of a large soil volume and the accessibility of water reserves in the soil which is important for most trees in maintenance of a stable water regime. Deficiency of water and nitrogen leads to a promotion of long root growth and restriction of side-root formation. This favors a fast penetration of the soil.

Because of technical difficulties, few attempts have been made to measure root growth continuously. Therefore little is known concerning maximal and average root growth rates of different trees under similar environmental conditions. The influence of defined environmental factors on root growth is still rather obscure. The data of different authors diverge widely because of different methods and conditions.

In Table II some data from our own measurements and from the literature are summarized. It can be seen that roots of fast-growing trees may reach values which are not inferior to that for herbaceous plants. Even the average values are considerable. It must be noted that the values measured in the root laboratory were obtained from newly planted trees. The disturbed root/shoot relation is normalized during the first year by preferential root growth, and a high incremental rate is reached. The "average" value means the average growth rate from all *growing* roots. This is not the average of the whole root system, because not all roots are growing at the same time. The data of different authors are not strictly comparable, but the differences in methods cannot be discussed here.

#### 4. DEPTH GROWTH

Little is known about the course of depth growth because excavations disturb root growth, and observations in Sachs-type root boxes are possible only for a short time and must be restricted to seedlings. In the root laboratory (Fig. 2) at Eberswalde<sup>1</sup> an adequate survey on time course, periodicity, and intensity of root growth could be obtained.

<sup>1</sup>Eberswalde is located at 52° 50' north latitude and 13° 49' east longitude; altitude 30 m above sea level; 572 mm annual mean precipitation (March, 38 mm; July, 81 mm); 8.4°C annual mean temperature; 18.8°C annual temperature variation.





FIG. 2. View into the interior of the root laboratory at Eberswalde. Removable panels permit observations of growing roots of trees. The above-ground parts are exposed to normal outdoor conditions. Soil temperatures and other parameters can be experimentally modified.

Characteristic differences in root development showed up in the first vegetative period after planting.

Because a homogeneously compacted sandy soil was used in the root laboratory, peculiarities of the tree species in depth growth were easily recognizable. In Figs. 3 to 5 the course of shoot and root growth are plotted for *Betula pendula* Roth., *Populus euramericana* "I 214," and *Pinus silvestris* L. Each point represents a growing root tip (see also Figs. 18 and 19 for *Robinia pseudoacacia* L.). It is obvious that depth development is very different in different species.

Whereas the roots of *Populus* and *Robinia* during the first vegetation period advance to a depth of 1.5 to 2 m, those of *Pseudotsuga taxifolia*, *Pinus silvestris*, and *Larix leptolepis* reach a depth of only 0.5 m. *Quercus borealis* var. *maxima* and *Betula pendula* go a bit deeper, whereas *Picea abies* remains shallower. Some values for maximal depth growth during the first vegetative period of comparable plants are summarized in Table II. The rate of depth growth is partly correlated with the general growth

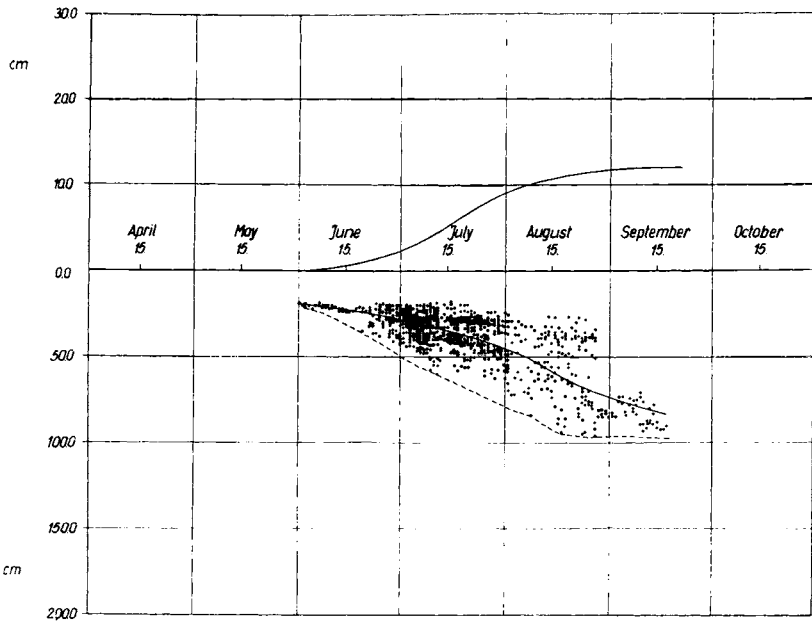


FIG. 3. Time course of depth growth of roots (bottom) and height increment of shoots (top) of 3-year-old *Betula pendula* (averaged data from twelve plants) during the first vegetation period in the Eberswalde root laboratory. Each dot represents a growing root tip. The solid line represents the mean depth increment of all growing roots; the dashed line shows the course of the maximal depth of root penetration (data from Hoffmann, 1966a).

rate of a tree species (see *Populus*, Fig. 4). Beyond that, specific differences exist in the rate of depth penetration. The fast depth growth of tree seedlings with taproots has already been mentioned. But some trees with typical heartroot, rather than taproot, systems for example, *Betula pendula* or *Robinia pseudoacacia*—soon reach even greater depths, which is very important for their water supply. Strong growth during youth means more than escape from shading. In some species deep rooting also diminishes danger from drought periods and so increases the ability of the species to compete. In *Betula papyrifera* shallow rooting on some sites leads to dieback (Pommerleau and Lortie, 1962).

Figures 3 to 5 show that as growth proceeds, the center of most active root growth (statistically represented by the solid line) shifts to deeper soil layers. This corresponds to the normal tendency of expansion of the root system under the influence of a specific correlative regulation. In virgin soils deviations are to be expected because of the irregular depo-

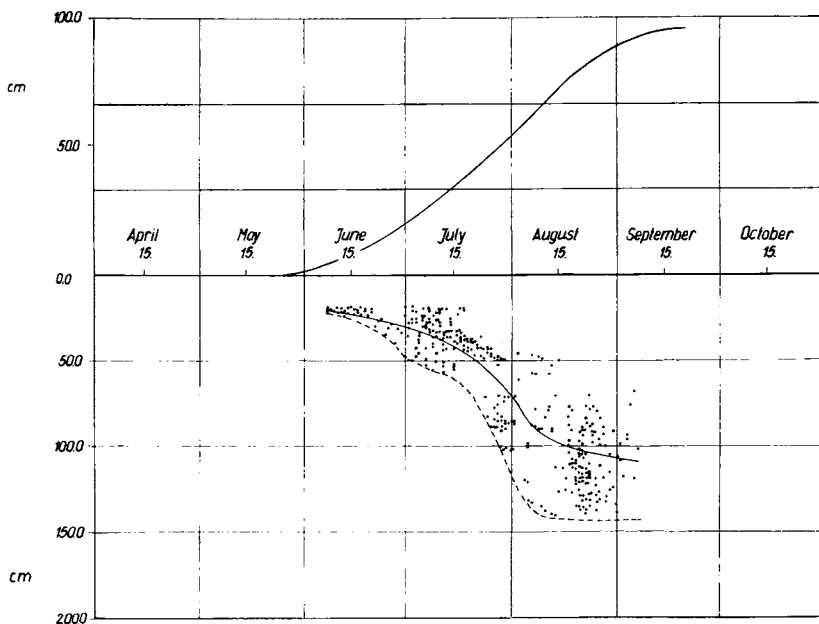


FIG. 4. Time course of depth growth of roots (bottom) and height increment of shoots (top) of 1-year-old *Populus euramericana* "I 214" (cuttings) during the first vegetation period in the Eberswalde root laboratory. Significance of curves and dots as in Fig. 3 (data from Hoffmann, 1966a).

sition of mineral salts. Their enrichment in the upper soil layers with high humus content leads to a concentration of fine roots in the upper horizons and thereby to a shallower rooting of most trees growing on such soils. Under ordinary outdoor conditions as much as 80 to 90% of the total mass of fine roots may be found in the upper soil layers (Coile, 1937; Scully, 1942; Hausdörfer, 1959).

In newly planted trees the tendency of the root growth center to shift to greater depths is very common. In older trees, which have fewer possibilities for further expansion of their root systems, other relations are found. In these, "growth nests" are formed around some strongly growing roots. Some roots stop growing and die; others form regeneration roots so that a more inhomogeneous growth distribution results. This can sometimes already be seen in the third vegetation period after planting, as, for example, in *Pinus silvestris* (Fig. 6). Here root growth starts and stops irregularly at different depths, and the density of growing roots is lower than in younger trees (although the total amount may be larger). Kinman (1932) made similar observations in orchard trees.

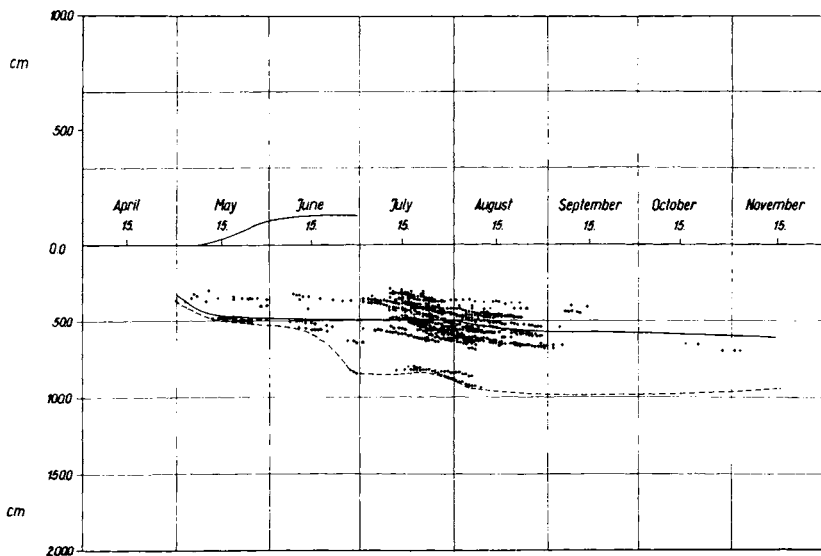


FIG. 5. Time course of depth growth of roots (bottom) and height increment of shoots (top) of 3-year-old *Pinus silvestris* during the second vegetation period in the Eberswalde root laboratory. Data presentation as in Fig. 3 (data from Hoffmann, 1966a).

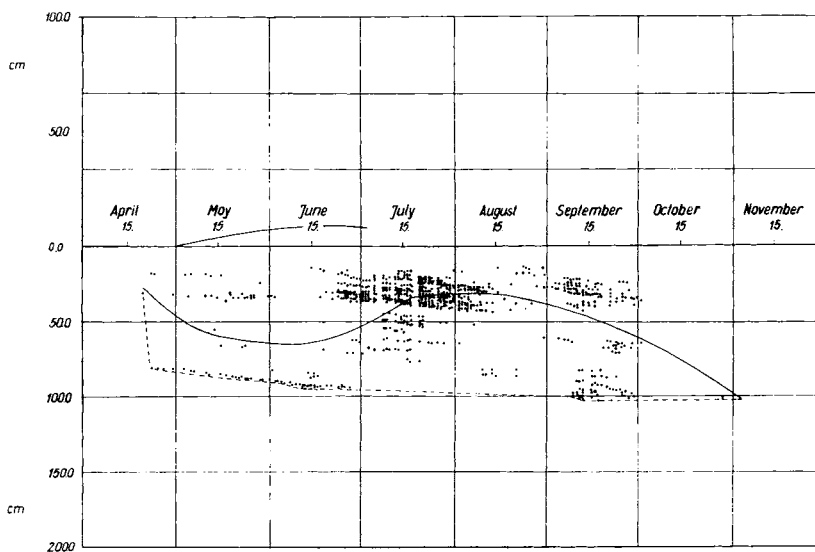


FIG. 6. Time course of depth growth of roots and height increment of shoots of 4-year-old *Pinus silvestris* L. in the third vegetation period after planting in the Eberswalde root laboratory. Data presentation as in Fig. 3 (data from Hoffmann, 1966a).

## 5. DENSITY OF ROOT SYSTEMS

Aside from the expansion of a tree's root system, its density is probably of great importance to the tree's ability to compete. In Figs. 3 to 5 (and in Figs. 18 and 19) distinct differences in the density of growing fine roots are evident. Penetration of the soil is very intensive in *Larix leptolepis*, *Betula pendula*, and *Pseudotsuga taxifolia*. A weak fine root formation is characteristic of *Quercus borealis* var. *maxima*, whereas *Robinia pseudoacacia* and *Populus euramericana* have an intermediate position. (In *Populus* the very fine hair roots with a diameter of less than 1 mm, which are typical of this species, were not registered. If these had been included the *Populus* root system would have been very much enlarged. See Table I.)

A low density may be compensated for by mycorrhizae formation, which is not considered here. The fine fungal hyphae may penetrate—more or less intensively, depending on the fungal species—the between-root soil spaces and thus make accessible nearly the whole soil volume of the root zone. However, this is of importance only in the upper soil layers, because frequency of mycorrhizae decreases with increasing soil depth (Preston, 1942; Werlich and Lyr, 1957). This may not depend on the humus content and the aeration of the soil, but seems to be caused by the physiological state of the different parts of the root system. For example, the nodule formation in *Robinia pseudoacacia* grown in the open and in the root laboratory shows very similar relations (Hoffmann, 1960; Lyr, 1963).

## 6. ACTIVITY IN SOIL PENETRATION

Tree roots are forced to penetrate large soil volumes, often against the mechanical resistance of densely packed soil layers, especially when the trees are acting as pioneer plants. In normal stands, young tree roots may follow old root channels formed by rotted roots or may grow in chinks of loam or other soil crevices and fissures. From practical experience it is well known that different tree species exhibit different activities in penetrating compacted or dense soil horizons, which on certain sites is the decisive feature for the choice of a tree species.

Results gained from comparable experiments on root activity, as the ability for penetration of dense soil layers is often called, are rare. An outstanding piece of work is that of Leibundgut *et al.* (1963) on the penetration of seedling roots through artificially made compacted clay layers in boxes. On the basis of measurements of the percentage of the total

root mass in the clay and in the loose layer beneath at the end of the vegetation period, the following sequence was determined: *Quercus robur* (26%), *Alnus incana* (8.7%), *Alnus glutinosa* (8.0%), *Carpinus betulus* (2.6%), *Picea abies* (1.6%), *Pseudotsuga taxifolia* (1.5%). This corresponds well to the ranking of root activity observed in the same species growing in the open. Species with a high root-to-shoot ratio seem to have a greater ability to penetrate hard soil layers. Gardner and Danielson (1964) in their experimental investigations found that optimal aeration of the soil and optimal water content of the root zone increased the ability of roots to penetrate.

#### 7. LONGEVITY OF FINE ROOTS

Statements and opinions expressed in the literature on longevity of fine roots are very divergent. According to Kinman (1932) fine roots may die, although only days old, when the base root begins to form periderm. In other cases longevity was estimated to be a few weeks (Childers and White, 1942). Heikurainen (1955) suggested, on the basis of his studies, a longevity of roots with diameters under 1, 1 to 2, and 2 to 5 mm of 3, 5, and 10 years, respectively. In general, fine roots seem to live at least through one vegetative period, which, however, on no account is the maximal age under favorable circumstances. In the root laboratory at Eberswalde, mycorrhizae and fine roots 2 years old, and older, could be observed. The longevity of fine roots depends partly on the correlatively regulated distribution of assimilates and partly on the growth intensity of the roots of higher rank. In the open a large fraction of the fine roots may be killed periodically by drought or frost, especially in the upper soil layers, so that frequent regeneration may consequently occur. This being the situation, it is obvious that any generally valid statements on the longevity of fine roots are difficult to formulate.

#### B. Periodicity of Root Growth

In addition to growth rate, growth periodicity of tree roots is also of scientific and practical interest. Whereas detailed information, and in some instances reproducible results, have been obtained on shoot growth, reports on root growth are in disagreement or are contradictory. At present it is still difficult to discriminate between peculiarities of species and environmentally induced reactions. For centuries investigations of the course of root growth have been made from a practical viewpoint, but owing to difficulties with techniques conclusions have been very vague.

Theophrastos of Lesbos (372–287 B.C.) observed that roots start growing before shoots in spring. Of the older works the following should be cited: Hales (1748), Du Hamel du Monceau (1758), von Dieskau (1776), G. L. Hartig (1808), König (1820), Lindley (1855), Th. Hartig (1863), von Mohl (1862), and Nobbe (1862). Comprehensive monographs have been compiled by Resa (1877), Wieler (1894), Engler (1903), MacDougal (1938), Ladefoged (1939), and Reed (1939).

The first contributions to our knowledge of root growth were in most cases based on casual observations during excavation or planting of trees. Systematic study of the subject was begun by Th. Hartig (1863) and Resa (1877). Hartig, specifically, gave the impulse for studies on morphological variations of the root system, and Resa for investigations on growth periodicity. Resa's method consisted in making periodic excavations of tree roots in their natural habitat to determine whether growth was or was not occurring. Similar methods were used later by Petersen (1898), Tolsky (1901), McDougall (1916), Stevens (1931), Reed (1939), Ladefoged (1939), and Vorobieva (1961).

Since the work of Stevens (1931) attempts have been made to get quantitative informations by marking the root tips. Of course only very incomplete information could be obtained by these methods because changes in soil structure and crushing and irritation of roots disturb their growth. When conclusions concerning active growth are drawn from the existence of white root tips, differences in browning of root tips introduces additional inaccuracies. Heikurainen (1955), Kalela (1955), and Kolesnikow (1962a) have periodically determined root weights from soil blocks and in this way have obtained indirect data on root growth.

Büsgen (1901) was the first to use root boxes for investigations on growth periodicity of forest trees. Because of size limitations only small plants can be investigated by this method. Nevertheless, it was employed later by Engler (1903), Crider (1928), Bodo (1926), Woodroof and Woodroof (1934), and L. M. Turner (1936). To permit continuous measurements of roots in their natural habitat Kinman (1932) and Rogers (1935) made trenches near orchard trees, set framed glass windows against the soil profile, and covered the pit between the measurements.

In our own investigations a root laboratory (Hoffmann 1966a) has proved to be valuable for plants from 3 to 8 years old. It consists of twelve root boxes (Fig. 2) measuring  $1 \times 1$  m, with a depth of 2.2 m. The construction of some of the root boxes allows the introduction of measurement instruments, application of chemicals, and taking samples

of roots or soils. Roots with diameters of 0.5 to 1.0 mm are measured at intervals of 1 to 2 days. Simultaneous determinations of the height growth of the main shoots are made. According to the size of the experimental plants, each root box contains 9 to 15 trees. Of course, only a part of the root system is visible through the glass panels; therefore measurements have in part been supplemented by determination of total amounts of root masses at the end of the vegetation period. Because of temperature differences and some influence of light, root growth in the interior of the box may be a bit different from the visible root growth. This had already been recognized by Engler (1903), but in the root laboratory these effects are of little influence. When trenches are used in the open, the regeneration arising from injured roots often gives a false picture of normal root growth (Kinman, 1932).

In all root growth measurements "longroots" have been used exclusively. These are the "Langwurzeln" of Büsgen (1901). Such roots have also been called "Triebwurzeln" (Bodo, 1926), "main roots" (Rogers, 1935), "growth roots" (Kolesnikow, 1962b), and "rope-like laterals" (McQuilkin, 1935). Growth measurements of roots of higher rank are extremely difficult because of their large number, their limited growth, and their small size. Here only determination of total weight gives reliable values.

#### 1. GROWTH INITIATION

In general, roots of trees in temperate latitudes have a period of rest in winter (this will be discussed in detail in the next section). Growth is resumed in spring. The starting time depends on the tree species and the weather. At present an exact theoretical base for a prognosis of the initiation of root growth from climatic data is still lacking. Richardson (1958), however, made a fairly successful attempt with *Acer saccharinum*.

For a general theoretical elucidation of root rest and growth resumption more experimental data are necessary. Probably it is a complex process, in which hormonal relations between root and shoot are very important, but hormonal regulation of root growth is in many aspects still obscure (Torrey, 1956; Romberger, 1963). Furthermore, knowledge of endogenously and exogenously influenced periods of dormancy of the individual organs of trees is limited.

Most authors agree that root growth starts before shoot growth, which was observed by Theophrastus 2250 years ago. Time between root growth initiation and expansion of swelling buds is extremely variable and de-



depends on environmental influences and on specific physiological optima. As detailed observations show, and the experiments of Richardson (1958) confirm, an impulse from the buds (which in this phase show a slight swelling) is necessary for root growth initiation. Apparently auxins are transported from the shoot to the root, which starts growing earlier because of a lower temperature optimum. According to Richardson (1958), roots of *Acer saccharinum* resume growth at 5°C, whereas bud expansion begins at 10°C. Similar differences probably exist in other tree species, but the absolute values may be expected to be different from species to species, and even from provenance to provenance. By February (in Central Europe) most trees have overcome endogenous dormancy and have entered postdormancy or the state of readiness (quiescence) in which temperature determines the time of bud opening. Increased soil temperatures lead directly or indirectly to earlier root growth, whereas bud expansion is not influenced (see Section II,C,1,a and Fig. 10).

The genus *Larix* is an exception to this general behavior, as was earlier demonstrated by the data of Engler (1903) and has been confirmed by our own measurements. In *Larix* species, needles of short shoots are unfolded long before root growth begins. These new short-shoot needles probably have the function of synthesizing the necessary assimilates for root and shoot growth, because reserve food storage in *Larix* is rather limited. Long-shoot expansion begins some time after needle unfolding and root growth initiation (Hoffmann, 1966a).

The beginning of root growth in *Quercus borealis* var. *maxima* is also relatively late. In Europe it may coincide with leaf unfolding. In most trees the first root growth is made at the expense of reserve materials. Therefore differences may exist between young seedlings and older trees in the continuation of root growth during shoot dormancy. Evergreen conifers, which can photosynthesize during winters, seem to behave differently from deciduous trees. In *Pinus silvestris*, root growth continues or is resumed independently of shoot growth when soil temperature is high enough (unpublished observations).

## 2. GROWTH PERIODICITY DURING THE VEGETATION PERIOD

Opinions on root growth rhythm during the vegetation period are very divergent. This is not surprising, if one takes into consideration the fact that the results were obtained from different tree species in different areas and climates and with different methods. Instead of the theoretical "normal distribution" or bell curve of mass increment, root growth as well as shoot growth has a very irregular time course (Figs. 7 and 8).

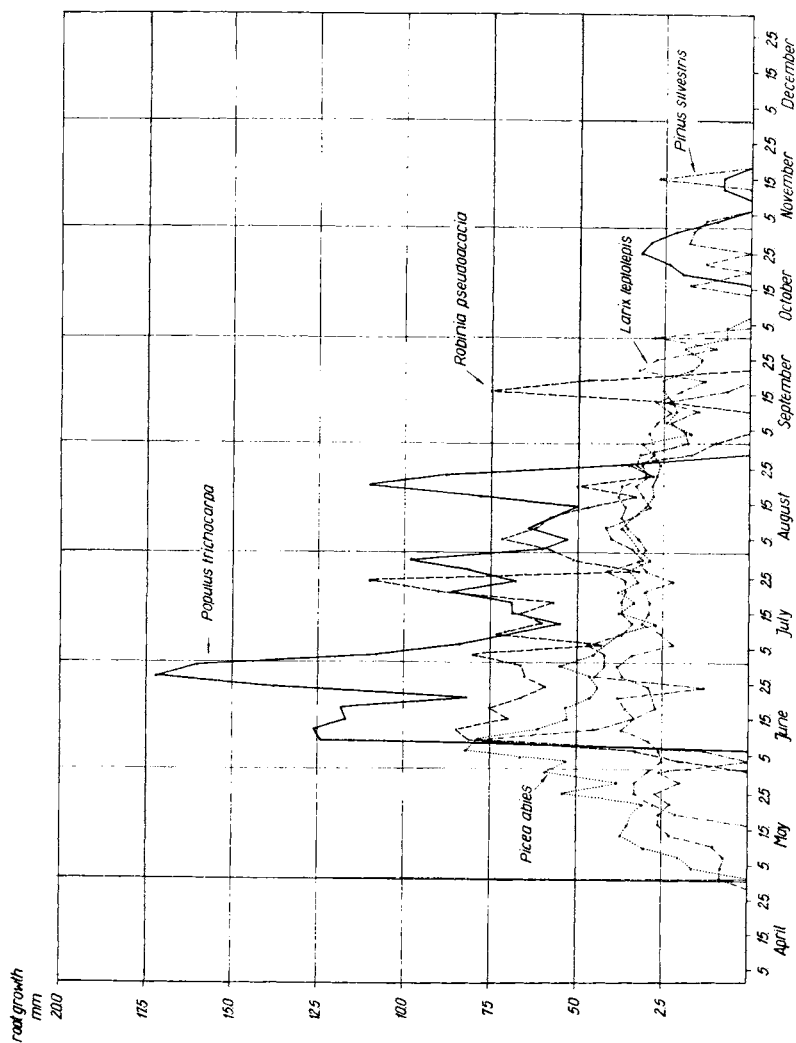


FIG. 7. Average rate of root growth of five tree species growing in the Eberswalde root laboratory; graphed points represent mean 3-day incremental values for all growing roots (data from Hoffmann, 1966d).

Resa (1877) assumed an antagonistic interrelation between root growth and shoot growth. This means that in months with strong shoot growth only a limited root growth or none at all should take place, and vice versa. In contradiction to this theory, Wieler (1894) and Büsgen (1901) pointed to a functional relation between root and shoot and argued that strong root growth must be bound to strong shoot growth. On the basis of comprehensive measurements Engler (1903) came to the opinion that in Central Europe all tree species have a maximum period of root growth in May and June, which is interrupted in August by a rest period, followed by a second but lower peak in autumn. Such a diminution or interruption of root growth in midsummer has often been described (McDougall, 1916; L. M. Turner, 1936; Kolesnikow, 1962b). But other authors (Tolsky, 1901; Hesselink, 1926; Rogers, 1935; Roze, 1937; Reed, 1939; Ladefoged, 1939) found no typical growth curves with two distinct peaks, which agrees with our own investigations.

We regard midsummer root growth cessation as due to unfavorable environmental conditions (periods of drought or high temperature). Under equivalent environmental conditions the rhythm of root and shoot growth differs from species to species and even from one individual tree to another. Some comparable curves for several tree species are summarized in Fig. 8. Because of the changing weather conditions, growth curves for different years are quite divergent, and generalizations are not yet possible. In our own measurements, neither significant antagonistic nor synergistic interrelations between shoot and root growth could be found by mathematical analysis. Interpretation is further complicated by the fact that at the same time growing and nongrowing roots may be found (Stevens, 1931; Ladefoged, 1939; Wilcox, 1954), so that their proportion should be determined. The correlation between environmental conditions and root growth is probably very complex, because besides direct influences of soil factors many indirect influences may act upon roots via primary effects upon activity.

Only the most general rules of root growth in a moderate climate can be stated here. Maximal root growth, with regard to both the number of growing roots and the total growth in length, in most tree species occurs in the early summer (June and July) (Fig. 8). Seedlings with early termination of shoot growth (*Quercus* type) often exhibited strong root growth in midsummer. Regarding the growth rate of individual roots, a maximum in early summer is evident, especially in deciduous trees (*Populus*, *Robinia*, *Quercus*, etc.), whereas conifers (*Pinus silvestris*, *Picea abies*, *Larix decidua*, and *Pseudotsuga taxifolia*) show a more uni-

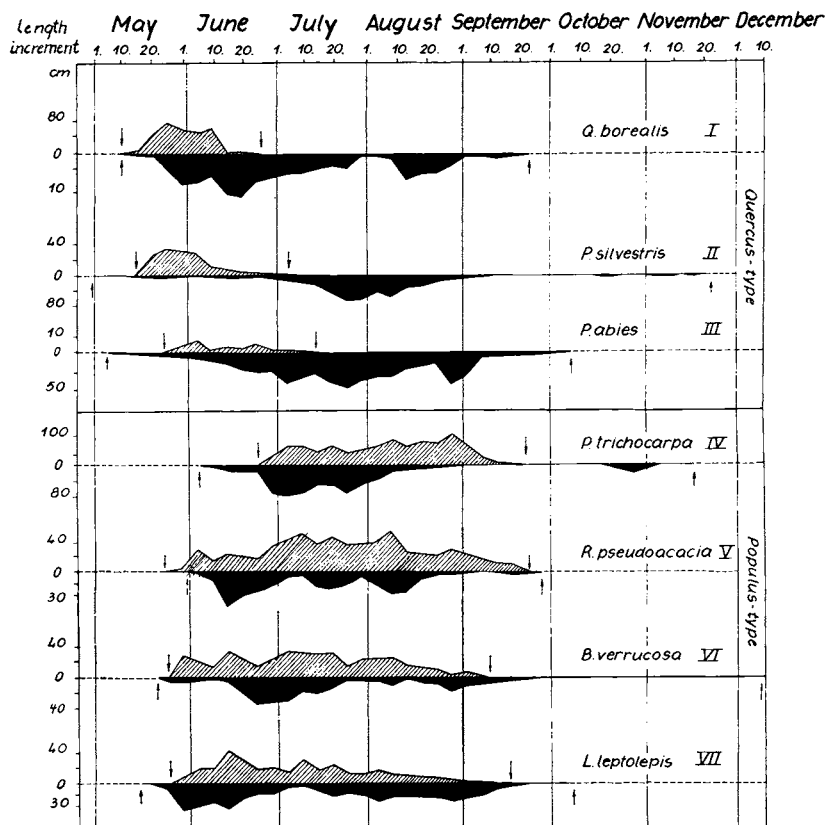


FIG. 8. Schematic diagram of the course of root growth and shoot growth of eight tree species in the Eberswalde root laboratory. Shading indicates shoot growth; solid black represents root growth; start and termination are indicated by arrows (data from Hoffmann, 1966d).

form growth throughout the whole vegetation period (Fig. 8). During August, but especially in September, root growth begins to diminish (Hoffmann, 1966a). Shoot growth in most species has stopped by the end of August or early September, often much earlier. Towards the end of the vegetation period the number of growing roots decreases considerably, and longer pauses in growth of individual roots can be observed. The measured values are often represented by only a very few roots.

Some species show peculiarities in root growth. For example, in *Pinus silvestris* root growth is very weak during the time of formation of new shoots and needles and increases considerably after expansion of the

needles. This may be true also in other *Pinus* species; it seems to be correlated with the strong consumption of assimilates by the growing shoot. During this growth phase negative balances of assimilation have been measured (Neuwirth, 1959).

### 3. TERMINATION OF ROOT GROWTH

In areas having low winter temperatures, root growth usually stops in the autumn. In the climates of Eberswalde, root growth of most trees ceases in September or October; only in some years does growth continue into November or even December. This was observed in 1963 in *Betula pendula* and *Pinus silvestris*. In all species root growth continues longer than shoot growth and can go on after leaf abscission. This is remarkable, because at this time (end of September or beginning of October) shoots are often already in deep dormancy (Vogl and Kemmer, 1961). Evidently there exists a certain autonomy of root growth, and it may be that—contrary to the condition in shoots—no internally controlled period of dormancy is present in roots. This is confirmed by observations that artificial heating of the soil extends root growth considerably (see Fig. 10) and that keeping of trees (*Pinus strobus*) in a warm greenhouse leads to continuous root growth (Stevens, 1931).

Several authors have described a winter growth of roots. This seems to be restricted to regions with mild winter temperatures and frost-free soils. It was observed for conifers and deciduous trees in the southern part of the United States, in British Columbia, in the Crimea, and in parts of Europe (Du Hamel du Monceau, 1758; Harris, 1926; Crider, 1928; L. M. Turner, 1936; Kolesnikow, 1962b). Apparently both evergreen trees and deciduous trees may have an uninterrupted root growth under certain circumstances. But in all cases a diminution of growth rate and the number of growing roots during the winter period has been reported.

### 4. DIURNAL GROWTH RHYTHM

Very few data exist on diurnal growth rhythms of roots. Kolesnikow (1962a) mentioned that growth should be stronger at night than during the day. Exact measurements in the root laboratory at Eberswalde have confirmed these statements. Although active root growth occurs during both day and night, it is more rapid at night. With day growth of a species taken as 100%, night growth of the same species gave on an average the following relative values: *Populus trichocarpa* 160; *Quercus borealis* var. *maxima* 137; *Pinus silvestris* 136; *Picea abies* 130. The diurnal rhythm of shoot growth is much more variable. Whether diurnal

growth rhythms are caused by internal periodicity or only by the externally regulated periodicity of photosynthesis, translocation, and transpiration has not yet been investigated.

### *C. Root Growth and Environmental Conditions*

#### 1. ROOT GROWTH AND SOIL TEMPERATURE

Because root growth, as well as mineral salt and water uptake, is dependent on metabolic processes, it is to be expected that soil temperature will influence root growth and activity and indirectly whole plant growth also. Shoots are dependent on roots for a sufficient supply of water, minerals, and some organic compounds. According to Tew *et al.* (1963), soil temperature has an even greater influence on transpiration than have air temperature and humidity.

Investigations on the effect of soil temperature on root growth are complicated by the fact that growth intensity of roots depends not only on temperature—as it might in heterotrophic microorganisms on an optimal medium, or in isolated roots in artificial culture—but also on soil moisture and shoot activity (carbohydrate supply), which are themselves influenced by light, air temperature and humidity, and root activity. Therefore no simple dependence of root growth rate on soil temperature can be expected under natural conditions. As our own measurements show, the rate of root growth during the vegetation period changes much more than soil temperature. The latter is a dominant factor only in spring and fall, because it acts together with other factors, such as soil moisture and shoot activity, during the summer.

Most authors agree that optimal temperatures for roots are lower than for shoots of the same species. This is demonstrated by the experiments of Richardson (1958), for example.

*a. Cardinal Temperature Values.* It is difficult to give useful values for minimum, optimum, and maximum temperatures for root growth of trees. Most authors have not distinguished between a physiological and an ecological optimum and have neglected the influence of other factors on these cardinal values. The method of measuring growth is very important in determining the temperature values. Therefore most data are not strictly comparable. Short-term measurements of root growth rates (Ladefoged, 1939) reveal the physiological optimum temperature (Fig. 9), which can also be obtained with isolated cultured roots. Ecological optimal values, on the other hand, are dependent on the carbohydrate balance and other factors. A long period of higher soil temperature can

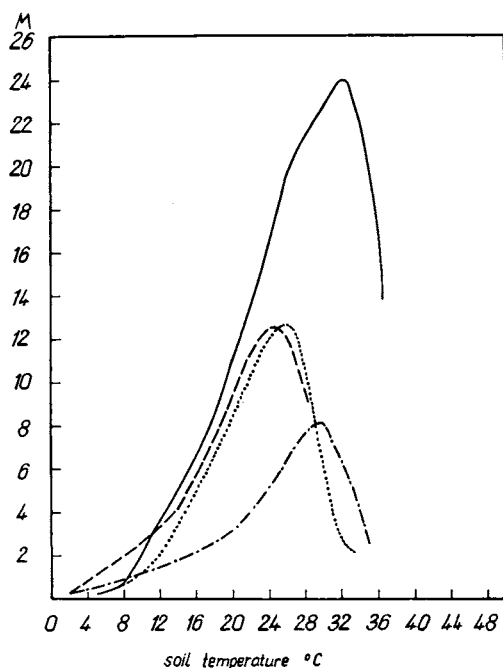


FIG. 9. Dependence of length growth of roots of *Fagus sylvatica* (-----), *Fraxinus excelsior* (-.-.-.-), *Picea abies* (.....), and *Abies alba* (——) on temperature ( $M$  = unit of increment) (after Ladefoged, 1939).

lead to a negative carbohydrate balance because of enhanced root respiration. In many cases the ecological optimum, therefore, lies below the physiological optimum. In Table III some cardinal temperature values from the literature are summarized. It can be seen from these data that the range of temperature in which growth is possible lies between  $+2^{\circ}$  and  $+35^{\circ}\text{C}$ .

Distinct differences in cardinal temperature values exist between species. This is probably true for provenances also. According to Aaltonen (1942), *Pinus silvestris* is more thermophilic in its root growth than is *Picea abies*.

The most exact data are those concerning the minimum temperature, because its determination from growth initiation or growth cessation is relatively simple. But even here the physiological and ecological values may be different. *Picea abies*, *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus* evidently have a rather low minimum. Growth begins or stops in the vicinity of  $2^{\circ}$  to  $4^{\circ}\text{C}$ . On the other hand, *Citrus* species

TABLE III  
CARDINAL VALUES OF TEMPERATURE FOR ROOT GROWTH SUMMARIZED  
FROM THE LITERATURE<sup>a</sup>

Tree species	Minimum tempera- ture (°C)	Optimum tempera- ture (°C)	Maximum tempera- ture (°C)	Authority
<i>Pinus strobus</i> L.	5-6	—	—	Engler (1903)
<i>Pinus cembra</i> L.	5-6	—	—	Engler (1903)
<i>Pinus mugo</i> Turra.	5-6	—	—	Engler (1903)
<i>Pinus taeda</i> L.	5	25	35	Barney (1951)
<i>Pinus silvestris</i> L. (in culture)	—	19	25	Slankis (1949)
<i>Picea abies</i> (L.) Karst.	2-4 <sup>a</sup>	26 <sup>a</sup>	—	Ladefoged (1939)
<i>Picea abies</i> (L.) Karst.	3-4	>10	—	Busarova (1961)
<i>Abies alba</i> Mill.	2-4 <sup>a</sup>	32 <sup>a</sup>	—	Ladefoged (1939)
<i>Larix decidua</i> L.	5.7	—	—	Ladefoged (1939)
<i>Fagus sylvatica</i> L.	>0 <sup>a</sup>	24 <sup>a</sup>	—	Ladefoged (1939)
<i>Fagus sylvatica</i> L.	2-3	—	—	Engler (1903)
<i>Acer pseudoplatanus</i> L.	2-3	—	—	Engler (1903)
<i>Fraxinus excelsior</i> L.	4-6 <sup>a</sup>	29 <sup>a</sup>	—	Ladefoged (1939)
<i>Betula</i> sp.	5	—	—	Vorobieva (1961)
<i>Malus</i> sp.	7.2 <sup>a</sup>	18.3 <sup>a</sup>	29.4 <sup>a</sup>	Nightingale (1935)
<i>Malus</i> sp.	4-5	—	—	Bodo (1926)
<i>Prunus domestica</i> L.	2-4	—	—	Bodo (1926)
<i>Prunus persica</i> (L.) Batsch.	7.2 <sup>a</sup>	18.3 <sup>a</sup>	29.4 <sup>a</sup>	Nightingale (1935)
<i>Prunus persica</i> (L.) Batsch.	—	24 <sup>a</sup>	35 <sup>a</sup>	Proebsting (1943)
<i>Citrus</i> sp.	—	24-27	—	Girton (1927)
<i>Citrus</i> sp.	11	—	—	Muromtsew (1962)
<i>Carya pecan</i> (Marsh.) Engl. & Graebn.	1-3 <sup>a</sup>	30 <sup>a</sup>	36 <sup>a</sup>	Woodroof and Woodroof (1934)
<i>Robinia pseudoacacia</i> L. (in culture)	—	22.5 <sup>a</sup>	—	Seeliger (1959)

<sup>a</sup> Experimentally determined values.

begin root growth only when the temperature rises above 11°C (Muromtsew, 1962). Roots of some *Malus* varieties and *Prunus persica* may even be called thermophilic.

A comparison of optimum temperatures from the literature is at present nearly impossible because physiological and ecological values are confused and the definition and determination of an ecological optimum are still obscure. Physiological data give information on the temperature at which the highest growth rate of roots has been observed, but it does



not follow that heating the soil to such a temperature would give an optimal effect on an ecological time scale. Here further investigations are needed.

It is striking that most physiologically optimal values lie above 20°C, temperatures which only rarely are reached in the soil. Although the ecological optimum may be lower than the physiological, it must be expected that on many sites soil temperature is suboptimal. In some cases it can even be the limiting factor. In our own experiments with *Robinia pseudoacacia*, artificial soil heating (increase of temperature about 5°C

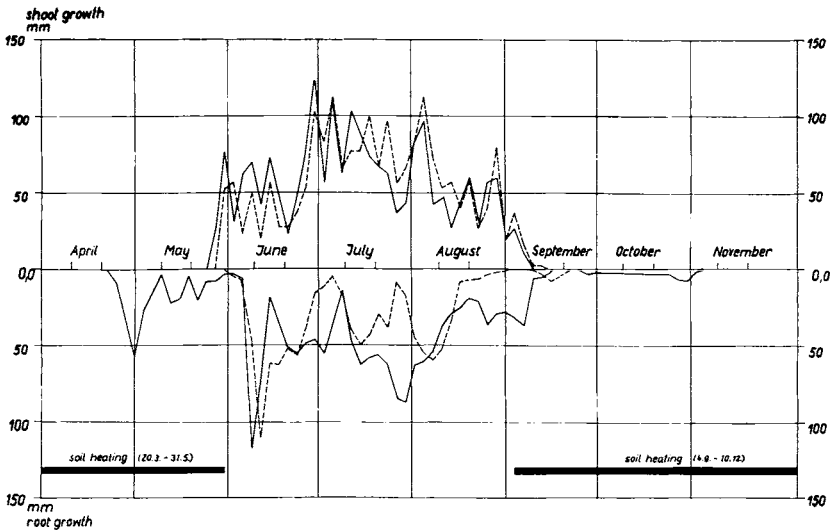


FIG. 10. Course of 3-day length growth of roots and shoots of *Robinia pseudoacacia* L. (3 years old) with additional soil heating (—) and of control plants grown under the same conditions but without soil heating (---) (root laboratory, Eberswalde, 1963) (data from Hoffmann, 1966b).

above normal) induced root growth which began 41 days earlier and terminated 44 days later than in control plants, whereas shoot growth (normal climate in the open) began only one day earlier (Fig. 10). The growth rhythm of the shoots in the two groups was similar, but the final height of shoots with soil heating was increased by 15% (11 cm). This effect seems to have been caused by the enhanced metabolic activity of the roots. Because *R. pseudoacacia* is a thermophilic tree species, further experiments are needed to show whether this is true for other species also.

In nurseries, soil mulching with plastic film can be used to increase soil temperature and conserve moisture. *Sorgum vulgare* showed an increase in yield of 68 to 76% after such treatment (Pusztai, 1963). However, no such data for tree species are yet available.

The effect of temperature on root growth is complicated by interrelations of root and shoot temperatures. Low root temperatures and high shoot temperatures favor shoot growth, and the inverse also holds, but high root or shoot temperatures can counterbalance low root or shoot temperatures to some extent (Hellmers, 1963).

The maximum temperatures are of practical importance only in special cases. In hot and dry regions (semidesert afforestations) root growth may be limited by high temperatures. This may also happen in temperate latitudes during dry periods in the season of strongest insolation. But here only shallow roots are directly influenced, and the danger of drought is more serious than that of heat.

Muromtsew (1962) pointed out the fact that plant species have a different amplitude of temperature for root growth. *Citrus*, for instance, belongs to a group with a small amplitude (7°C), whereas strawberries have a wider one (16°C). This seems to be related to the normal climatic temperature amplitude of the indigenous region. Therefore it is to be expected that trees from the tropics and subtropics should have a narrow amplitude, and trees from temperate and cold regions a progressively wider amplitude. At present, exact and comparable values are lacking. But it seems possible that site tolerance of a species can be limited by the soil temperature, which is especially important in the cultivation of exotic trees. Insufficient root activity as a consequence of low soil temperatures could be a reason for the natural tree line in the alpine and northern regions, because plants suffer from desiccation due to high transpiration and limited water uptake (Michaelis, 1934).

It should be mentioned that temperatures induces morphogenetic changes in roots. Isolated roots of *Robinia* show an inhibition of lateral root formation at 19°C and an inhibition of length growth of the main root at 33°C, which favors side-root development (Seeliger, 1959). Similar results were obtained by Slankis (1949) with *Pinus silvestris*. Nightingale (1935) observed that roots of peaches were glistening white with large-diameter, succulent, and fragile tips when grown at 24°C. Roots of *Sequoia* seedlings appeared to be the healthiest, but not the longest, at 18°C. They were short and thick at 8°C, and thin with fewer and shorter white root tips at 28°C (Hellmers, 1963).

## 2. ROOT GROWTH—SOIL MOISTURE AND SOIL AERATION

Besides soil temperature, soil moisture influences root growth considerably. Useful growth measurements are complicated by the fact that the water uptake by an individual root does not determine its growth rate. A sufficient water uptake by a part of the root system can provide the necessary water for the whole system. Therefore some roots of a system can grow through dry zones when an internal water supply is guaranteed by water uptake of other roots (Shautz, 1927; Kausch, 1959). Because of the unequal distribution of moisture in the soil, this fact is of considerable ecological significance. Of course, mineral salt absorption is inhibited in dry soil zones, as was demonstrated by Hunter and Kelley (1946) with  $P^{32}$ .

Water deficiency and water surplus, both have a large influence on the formation of the root system and its activity. In general, root systems are plastic enough to adapt to slowly changing soil water conditions (Rubner, 1960), but rapid changes of the ground-water level can lead to serious root damage because it takes some time before an older root system can adapt to new conditions (Heikurainen, 1964). In soils with high ground-water level we find a "surface," "disk," or "pancake" root system, not only in trees with a natural tendency to form these (*Picea abies*) but in most other species also.

*a. Water Deficiency.* Experimental investigations on the influence of soil moisture on root growth have been very infrequent. Therefore nothing is known about specific limit values. Reed (1939) found no significant connection between soil moisture and root growth and stated only generally that growth decreased at low moisture contents. According to Kaufman (1945), daily length growth of *Pinus banksiana* roots decreased from 3.2 mm (July) to 1.2 mm (August) as a consequence of the diminishing of the soil water from 11% to 2% of capacity. According to Ladefoged (1939), root growth stops in most species when soil moisture is reduced to 12 or 14% on an oven-dry soil basis (or 4 to 6% on an air-dry soil basis). An increase of moisture content above 40% induces almost no additional growth increment (Fig. 11).

In dry soils, roots have a tendency to grow toward more humid zones, so that root enrichments are observed in such zones. In dry soils roots are found at greater depths than in moist soils (Jocum, 1937; Polanskaja, 1962). In silvicultural plow-furrow plantings, fine roots of young pines are restricted to the furrows, presumably because of their higher water

content (Buchholz and Neumann, 1964). On the other hand, roots avoid areas of excessively wet soil (Howard, 1925). Roots in swamps lie near the surface, and root growth in depth depends on changes in the ground-water level (Busarova, 1961).

In dry soils the root system has a higher portion of the total plant weight. With increasing soil moisture content the root portion decreases in favor of the above-ground organs (Tolsky, 1904; Aaltonen, 1920; Huber, 1924; Rogers and Vyvyan, 1928; Volk, 1934). In drier soils not only is a larger soil volume made accessible for water absorption by an extensive

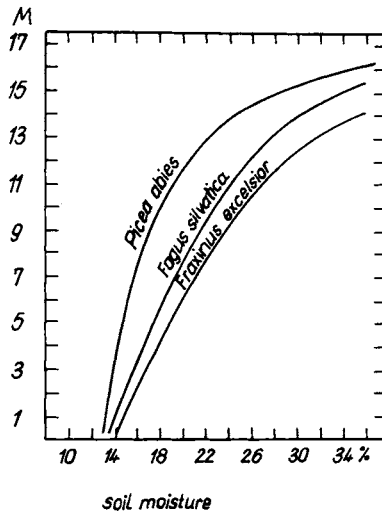


FIG. 11. Dependence of root length growth on soil moisture. Moisture content is given in percentage of oven-dry soil weight (data from Ladefoged, 1939).

root system, but the chances of roots encountering scattered local areas of higher water content are also increased. The root system can begin growth anew during drought periods if parts of the system are wetted, thereby increasing the internal water supply to all the roots (Bormann, 1957; Kausch, 1959). Water deficiency leads to an inhibition of root growth before cessation of shoot growth or any visible injury becomes evident (Rogers, 1935; L. M. Turner, 1936; Ladefoged, 1939; Leyton and Rousseau, 1958; Kokhno, 1959). Figure 12 shows this behavior for *Larix leptolepis* in Germany during the drought of 1964.

Root suberization is accelerated in dry soil and the effective absorbing surface is thereby diminished, so that root systems do not regain their full capacity for water uptake rewetting until some regeneration of

growing tips has occurred (Kramer, 1950). When the soil becomes very dry, parts of the root system may die. This is common in surface soil layers (Buchholz and Neumann, 1964). Therefore water and mineral salt uptake remains diminished even for a long time after conditions return to normal following a severe drought. This, in turn, retards root regeneration by inhibition of photosynthesis and brings long-lasting growth depressions in older stands.

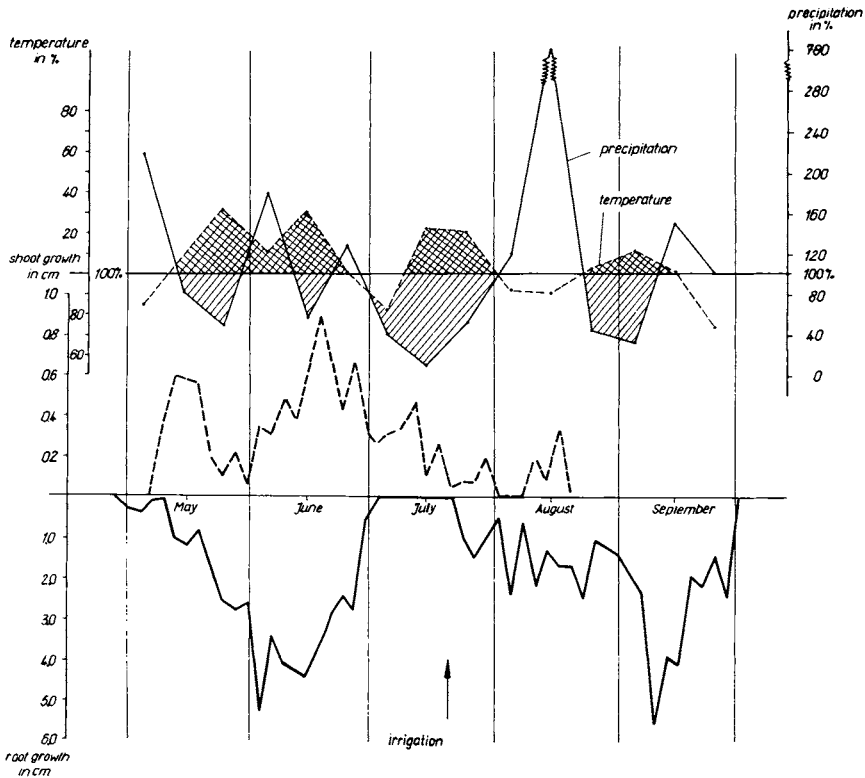


FIG. 12. Behavior of root and shoot growth of *Larix leptolepis* during the drought period of 1963. Precipitation and air temperature are expressed in percentage of deviation from the long-term mean value (data from Hoffmann, 1965).

*b. Water Surplus.* Some sites suffer permanently (swamps and peat bogs) or intermittently (flood plains) from an excess of water in the soil. Water excess—especially in connection with slow water movement—implies a low oxygen availability in the soil. As the results of artificial water cultures demonstrate, tree roots are in general not sensitive to water saturation of the medium, provided that sufficient aeration is main-

tained. However, ordinarily water saturation of the soil results in a deficiency of oxygen and an enrichment of carbon dioxide, which shifts the redox potential. Furthermore, wet soils are apt to be cold. This lowers the mineral salt and water uptake (Kramer and Kozlowski, 1960); therefore, flooding or raising of the ground-water level inhibits growth or induces dieback in susceptible tree species as an indirect consequence of an insufficient root activity. Symptoms often first appear during a subsequent drought period, when water supply to the shoot by the partly dead or injured root system is inadequate. Dieback of tree stands in large areas may set in when, because of oxygen deficiency, reduced compounds are formed in the soil which poison the roots ( $\text{H}_2\text{S}$  from peat, for example) (Trenel, 1932). On peat bogs, as well as on frozen soils, severe symptoms of mineral salt deficiency are common, although often mineral salt content of the soil is not particularly low.

Roots in swamps are relatively long and poorly branched. After draining of the soil, length growth diminishes, branching increases, and sinker roots are formed which reach greater depths (Heikurainen, 1964). In soils of low moisture content fine roots are usually densely branched.

c. *Soil Aeration*. Excess water in the soil causes reduced gas exchange between soil and atmosphere so that, by the respiration of soil microorganisms and roots, oxygen content decreases and  $\text{CO}_2$  and other metabolic products increase. Whether decrease of oxygen or increase of  $\text{CO}_2$  is more important for root growth is judged differently by various authors. Considerable differences between the tree species probably exist. Boynton (1940) mentioned that at 5%  $\text{CO}_2$  new formation of roots of apple trees is so strongly disturbed that shoot growth is depressed.

Negative effects on growth of agricultural plants by only 1 to 2%  $\text{CO}_2$  in the soil atmosphere were described by Lundegårdh (1957). On the other hand, astonishingly high  $\text{CO}_2$  concentrations can be tolerated by tree roots if an adequate oxygen supply is provided. This may be as high as 45%  $\text{CO}_2$  in *Salix* according to Cannon and Free (1925), or 15 to 60% in cotton according to Leonard and Pinckard (1946). Because of such tolerance, Voigt (1962) considers oxygen the more important factor. According to Leyton and Rousseau (1958) the oxygen requirement is different from species to species (Fig. 13). In *Picea nigra* even differences between provenances could be demonstrated.

Root growth in *Pinus* and *Picea* is noticeably inhibited at values around 10%  $\text{O}_2$ . Cannon and Free (1925) regarded 8 to 10%  $\text{O}_2$  as minimal for good root growth. In *Malus*, root growth is already detectably

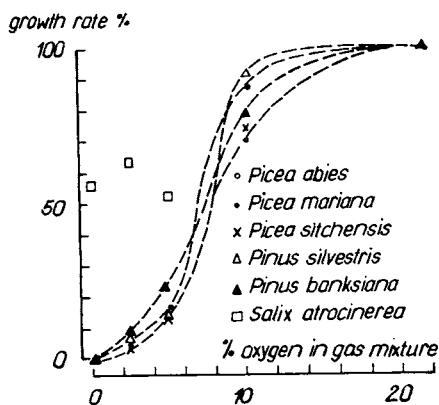


FIG. 13. Influence of aeration of rooting medium on root growth. Root growth expressed as percentage of that with normal aeration (after Leyton and Rousseau, 1958).

reduced at 15%  $O_2$ ; at 3 to 5% poor growth still can be observed; and at 0.1 to 3% the minimum is reached (Boynton, 1940; Boynton and Reuther, 1938). Only a few species can grow when available oxygen falls below 2% of the soil atmosphere (Fig 13). In the absence of oxygen, roots die after some time. Growth periodicity is of importance in so far as the oxygen requirement during dormant or inactive periods is lower and tree roots are less sensitive. *Salix*, *Alnus*, *Betula*, and some other genera probably are able to provide their roots with some oxygen through an intercellular space system, enabling these species better to tolerate sites poor in soil oxygen (Huikari, 1954; Leyton and Rousseau, 1958). This principle is extremely effective in water and swamp plants which have a large intercellular space system (aerenchyma). In the environs of roots with an internal oxygen supply, heavy metal sulfides in the soil are reoxidized.

Trees are limited in their ability to colonize frequently flooded or swampy soils mainly by their relative ability to maintain root growth and adequate root metabolism under conditions of poor oxygen supply and lower temperatures (Barner, 1954, 1965). Some trees have developed organs especially adapted for gas exchange in roots (*Sonneratia*, *Bruguiera*, and *Taxodium* species). According to Coster (1933) the resistance of tropical trees to oxygen deficiency in the soil is highly variable. Roots of deep-rooting species are said to have lower oxygen requirements, and oxygen requirements of roots may be an important factor in competition in the tropics (Eidmann, 1935).

### 3. ROOT GROWTH AND MINERAL NUTRITION

Mineral nutrition also influences root growth and root morphology. In spite of numerous accounts in the literature, it is seldom clear whether the effects described are unspecific and resulting from general promotion of plant growth (for example, as a consequence of fertilization), or whether there are specific influences of mineral nutrition on root growth (Mengel, 1965). The latter have been indicated in some instances, but in general it must be observed that mineral nutrition is closely related to other growth factors such as water supply and shoot activity, and effects of mineral nutrition per se are difficult to ascertain.

It is well known that root development in poor soils is comparatively stronger than in rich ones (Schwarz, 1892; Büsgen, 1901; Rogers and Vyvyan, 1928). The root-to-shoot ratio may be nearly 1 : 1 in poor soils, whereas it decreases in better soils to about 1 : 2. Zöttl (1964), therefore, with only moderate simplification, states that in vigorously growing stands increased increments of stem wood after fertilization are obtained with unstimulated or only slightly increased root systems. On the other hand, in nutritionally poor stands, additional growth of above-ground parts requires a strong enlargement of the root systems.

A striking fact is the concentration of fine roots in nutrient-rich zones of the soil. Thus stimulated root growth in soil layers rich in humus is often recorded in the field (Möller, 1903; Albert, 1928; Wagenknecht, 1941; Grunert, 1955; Hausdörfer, 1959). In part this may be a nitrogen effect, as it is particularly evident in soils poor in nitrogen (Ehwald *et al.*, 1963). But evidently other nutrients also act in a similar way, because the same phenomenon can be observed in layers of coarse sand with high contents of silicates and in strata of clay or heavy minerals (Fig. 14). A direct influence of soil moisture, although sometimes strengthening the effect, may be excluded. This behavior is caused by the general reaction norm of the root system, which in a state of nutrient deficiency primarily forms poorly branched long roots ("seeking or "pioneer" roots).

In soil layers rich in nutrients, the growth of the main root is lessened at the expense of a strengthened development of side roots, resulting in dense root development in these layers (Fig. 15). This antagonistic behavior between length growth and side-root development is a characteristic feature (Kausch, 1959) which results in ecologically useful modifications of root systems under the influence of certain site factors. Furthermore, it explains the observations that the rooting quotient (total root length/number of root tips) of orchard trees is very high in sandy soils



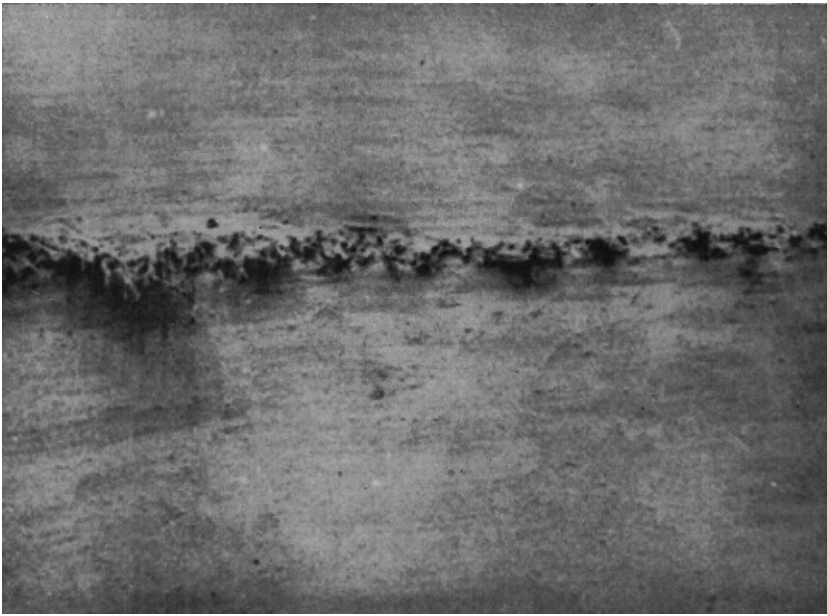


FIG. 14. Concentration of *Pinus silvestris* roots in a layer rich in heavy minerals in a poor sandy soil (after Kundler, 1956).

and is reduced after fertilization (Otto, 1964). Various clones, however, may react somewhat differently in this respect. Lundegårdh (1957) suggested that the favored length growth induced by nitrogen deficiency be called "nitrogenium-deficiency-etiolement."

In addition to the above, it must be noted that the mineral nutrient status (and especially nitrogen supply) affects the root-to-shoot ratio. Therefore, in the field, differences occur in intensity of rooting in various humus forms with different nitrogen contents (Table IV). In raw humus

TABLE IV  
ROOT LENGTH AND WEIGHT PER SQUARE CENTIMETER OF LEAF AREA OF BEECH  
PLANTS GROWN IN DIFFERENT TYPES OF HUMUS  
(Data from Meyer, 1963)

Humus form	Root length (cm/cm <sup>2</sup> )	Root weight (gm/cm <sup>2</sup> )
Mull	6.29	7.28
Moss humus	7.78	7.65
Raw humus	15.90	12.40

poor in nitrogen, *Fagus silvatica* forms about twice as much length and weight of roots per square centimeter of leaf area as in mull (Meyer, 1963).

Humic acids and quinoid compounds have been reported to elicit specific plant growth effects. Stimulation of root growth has also been

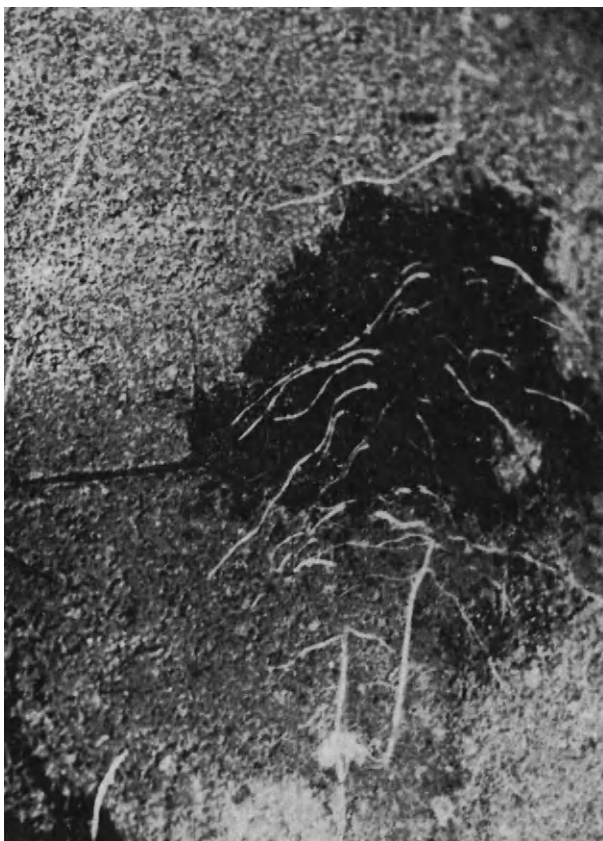


FIG. 15. Root formation of *Betula pendula* in a sandy soil with an artificial humus pocket. Note the intensive branching and fine root formation in the humus (from the root laboratory at Eberswalde).

reported (Flaig, 1958; Giulimondi, 1961). Little is known about the possible effects of other biogenic compounds formed in the soil on root growth and development.

Specific effects of different nitrogen compounds are noteworthy.

Leyton (1952), Prjanischnikow (1952), and Smith (1957) found that the root systems of plants supplied only with nitrate are stronger than of those plants fertilized with ammoniacal nitrogen. Evers (1964) also considers nitrate to be the best form of nitrogen for growth of poplar. *Alnus glutinosa* fertilized with nitrate develops very dense, fine, and abundantly branched root systems, whereas ammoniacal fertilization causes formation of long and sparingly branched roots. Under field conditions there is probably a relation between soil aeration and the form of soil nitrogen.

An extensive and rather contradictory literature exists concerning the effects of other elements on root growth and the formation of root

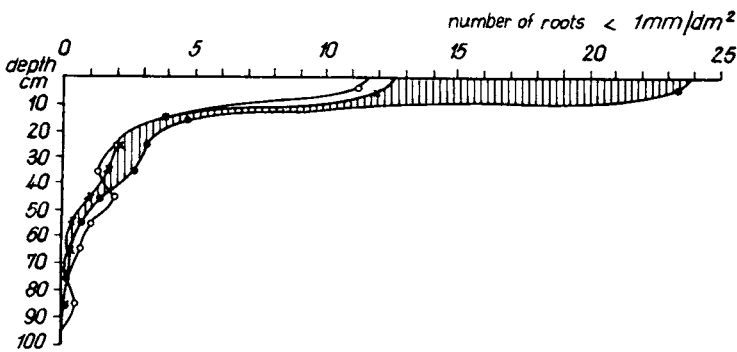


FIG. 16. Root development after fertilization in a stand of *Pinus silvestris* on a devastated sandy soil of average productivity. Represented as number of roots less than 1 mm in diameter per 1 dm<sup>2</sup> wall area of soil profile: 0 — 0 = 54-year-old stand without fertilization; X — X = 57-year-old stand without fertilization; .-.- = 57-year-old stand fertilized in 1962 with N-P-K and Mg (80 kg of nitrogen per hectare) and in 1963 with 80 kg of nitrogen per hectare (data from Buchholz and Neumann, 1964).

systems. Because of ion antagonism and multifactorial effects which may lead to variable results in different cases, valid generalizations for woody plants are not yet possible. (For further literature see Kramer, 1956.) Fertilization of forests generally stimulates superficial rooting because vertical translocation (especially of phosphorus) is rather slow. Furthermore, the humus content and the recycling of nutrients by soil organisms favor the enrichment of nutritive elements in the upper soil horizons. Buchholz and Neumann (1964) found that in a 56-year-old pine stand the superficial rooting was doubled two years after nitrogen fertilization, while at the same time the deep rooting decreased (Fig. 16).

TABLE V  
INCREMENTS IN DRY WEIGHT OF FIVE TREE SPECIES IN POTS DURING ONE VEGETATION PERIOD IN THE OPEN  
UNDER DIFFERENT LIGHT INTENSITY CONDITIONS  
(Data from Lyr *et al.*, 1963)

Tree species		Shading degree as per cent of full light							
		I		II		III		IV	
		100-85%		70-55%		45-30%		15%	
		gm	%	gm	%	gm	%	gm	%
<i>Quercus borealis</i> var. <i>maxima</i> (Marsh.) Ashe									
Total weight	—	—	—	6.89	—	7.38	—	6.67	—
Weight of leaves	—	—	—	1.14	—	1.14	—	1.12	—
Weight of shoot axes	0.69	100	181	1.25	181	1.32	191	1.22	177
Weight of roots	1.91	100	240	4.59	240	4.93	258	4.35	228
Total weight of roots and shoot axes	—	100	210	—	210	—	224	—	202
<i>Pseudotsuga taxifolia</i> var. <i>viridis</i> (Poir.) Britt.									
Total weight	0.33	100	2.00	606	1.74	527	1.39	421	1.03
Weight of needle and shoot axes	0.25	100	1.00	400	0.85	340	0.70	280	0.65
Weight of roots	0.08	100	1.00	1250	0.89	1113	0.69	863	0.38
Total weight of roots, needles, and shoot axes	—	100	—	825	—	726	—	571	—
<i>Pinus silvestris</i> L.									
Total weight	0.60	100	2.28	380	1.62	270	1.74	290	1.02
Weight of needle and shoot axes	0.51	100	1.51	296	1.04	204	1.17	229	0.84
Weight of roots	0.09	100	0.77	856	0.58	644	0.56	622	0.19
Total weight of roots, needles, and shoot axes	—	100	—	576	—	424	—	436	—

*Betula pendula* Roth.

Total weight	—	—	2.35	—	2.23	—	2.16	—	0.98	—
Weight of leaves	—	—	0.48	—	0.47	—	0.44	—	0.32	—
Weight of shoot axes	0.34	100	0.83	244	0.75	221	0.75	221	0.36	106
Weight of roots	0.31	100	1.04	335	1.01	326	0.97	313	0.31	100
Weight of roots and shoot axes	—	100	—	290	—	274	—	267	—	103

*Alnus glutinosa* L.

Total weight	—	—	18.35	—	9.55	—	7.26	—	5.03	—
Weight of leaves	—	—	3.07	—	1.76	—	1.53	—	1.19	—
Weight of shoot axes	1.21	100	4.56	377	2.62	216	2.25	186	1.61	133
Weight of roots	0.93	100	10.36	1114	4.98	535	3.35	360	2.13	176
Weight of roots and shoot axes	—	100	—	746	—	376	—	273	—	154
Weight of nodules	—	—	0.35	—	0.20	—	0.13	—	0.10	—

## 4. ROOT GROWTH AND LIGHT INFLUENCE

The formation of the root system is dependent—as is plant growth as a whole—on the photosynthetic efficiency of the tree, which means that root growth is in competition with shoot growth for carbohydrates. In higher plants a general and ecologically useful reaction norm in the distribution of carbohydrates has evolved, especially when shading makes

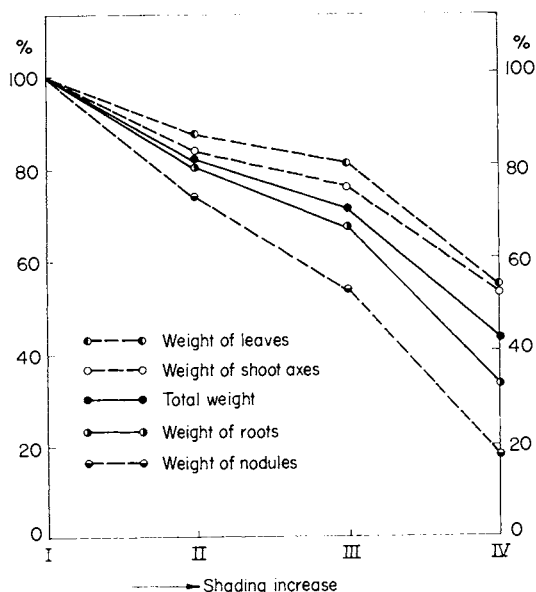


FIG. 17. Relative changes in weight of individual plant organs and of the total plant weight under the influence of different light conditions (Mean values of *Pinus silvestris*, *Pseudotsuga taxifolia*, *Betula pendula*, *Robinia pseudoacacia*, *Alnus glutinosa*, and *Quercus borealis*) I = 85 – 100%, II = 55 – 70%, III = 30 – 45% and IV = 15% of full daylight (after Lyr *et al.*, 1963).

carbohydrates limiting. Increasing shade decreases growth as a whole but leads to a relative stimulation of shoot growth at the expense of root development (Fig. 17, Table V) (Mitchell, 1936; Gast, 1937; Kozłowski, 1949; Lyr *et al.*, 1963). In short, shading primarily influences root growth, and the root-to-shoot ratios are thereby altered (Table VI).

The intensity of the effect, however, varies according to the shade tolerance of the species involved. From this it is clear that at reduced light intensities the ability to wage root competition decreases in shade-intolerant species. This effect may be reinforced by other factors that

TABLE VI  
ROOT INCREMENT AND ROOT-TO-SHOOT RATIOS OF FIVE TREE SPECIES AS AFFECTED BY VARIOUS DEGREES  
OF SHADING DURING ONE GROWING SEASON<sup>a</sup>  
(Data from Lyr *et al.*, 1964)

Degree of shading	Light inten- sity	<i>Pinus silvestris</i> L.		<i>Larix decidua</i> L.		<i>Picea abies</i> (L.) Karst.		<i>Fraxinus excelsior</i> L.		<i>Tilia cordata</i> Mill.	
		A	B	A	B	A	B	A	B	A	B
0	100%	130	(0.47) 100%	157	(0.58) 100%	182	(0.57) 100%	150	(1.03) 100%	139	(0.98) 100%
I	68%	180	(0.46) 98%	—	—	159	(0.57) 100%	127	(1.01) 98%	171	(1.18) 120%
II	35%	100	(0.41) 87%	122	(0.55) 95%	145	(0.67) 118%	124	(0.96) 93%	167	(1.08) 110%
III	12%	0	(0.28) 60%	13	(0.46) 79%	59	(0.43) 75%	55	(0.87) 85%	72	(0.93) 95%
IV	1% dead	dead	—	dead	—	-16	(0.33) 58%	-4	(0.64) 62%	18	(0.84) 86%

<sup>a</sup> A = root increments in per cent of initial weight; B = root-to-shoot ratios, both absolute and as percentage of initial.

induce a relative reduction of root growth—for example, nitrogen fertilization (Lyr *et al.*, 1967). Shaded plants are therefore apt to be more susceptible to drought than others in full light (Kramer and Decker, 1944; Barney, 1951). At a light reduction to 40% of daylight, which is by no means an extreme shading degree under field conditions, both rooting depth and rooting density of *Robinia* are strongly reduced (Figs. 18 and

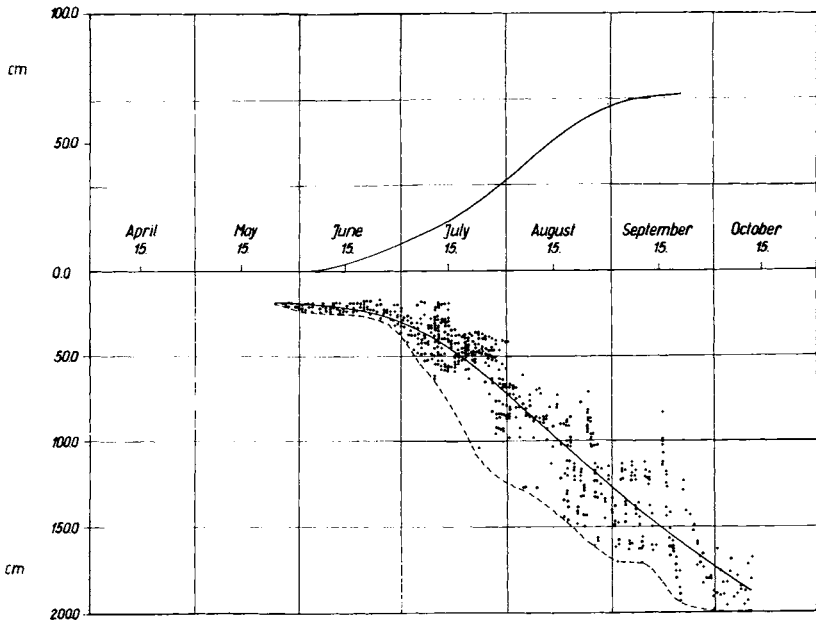


FIG. 18. Course of root depth growth and shoot height increment of *Robinia pseudoacacia* (2 years old) in full daylight. Data presented as in Fig. 3 (data from Hoffmann, 1966a).

19). Whereas plants in full daylight showed a total length of fine roots of 266 m, the corresponding value in the shaded ones was only 39 m (Hoffmann, 1965). In *Lupinus* and *Alnus*, shading greatly reduces nitrogen fixation (Hoffmann, 1960; Lyr *et al.*, 1963). Some other tree species show remarkable reduction in formation of mycorrhizae when shaded (Björkman, 1942).

W. Turner (1922) and Shirley (1929) earlier pointed out that the strongest root systems are developed in full daylight. The former believed that surplus quantities of assimilates not required for shoot growth are used for root growth. This may be only partly correct, however. If a



sufficient nitrogen supply is provided, shoots compete with roots whenever environmental conditions allow growth. Whether trees of the *Populus* type, having long duration of shoot growth, and of the *Quercus* type, which have a short growth period (Lyr and Hoffmann, 1965), behave differently in root/shoot competition has not yet been determined.

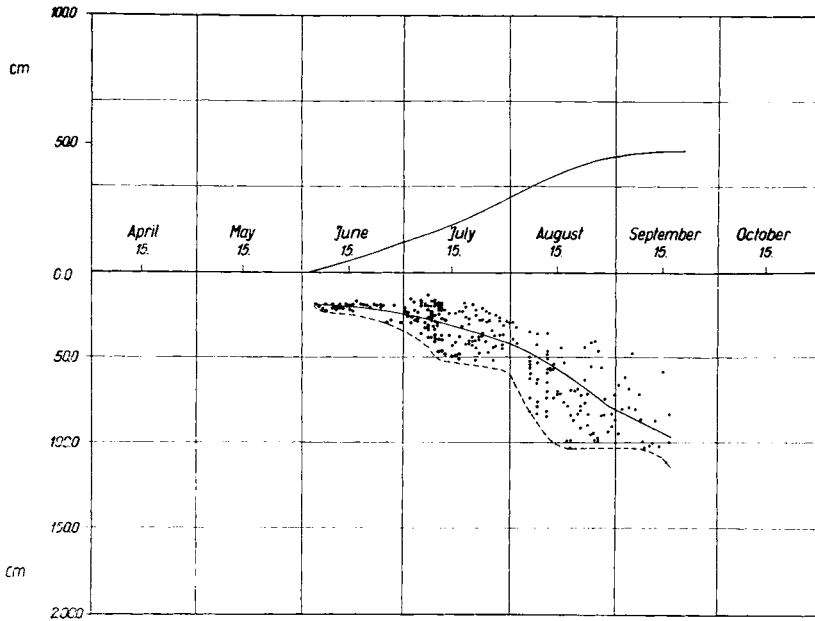


FIG. 19. Course of root depth growth and shoot height increment of *Robinia pseudoacacia* (2 years old) with natural light diminished by 60%; otherwise comparable to Fig. 18 (data from Hoffmann, 1966a).

Reduction of photosynthetic activity, although caused by shading of the leaves, results in decreasing root growth, but not immediately. The reaction of the roots takes place after 12 to 24 hours in *Acer saccharinum* (Richardson, 1953a,b). This may be the reason why root growth is more active at night than during the day (Section II,B,4). In young *Acer* seedlings this root reaction is more rapid, whereas in *Quercus* the reaction of root growth as a consequence of shading takes place more slowly, presumably because of higher food reserves in this genus (Richardson, 1956). The negative phototropism of roots is well known. But various species are likely to exhibit different sensitivity. Isolated roots of some tree species show decreased growth in the light (Seeliger, 1959).

## 5. ROOT/SHOOT INTERRELATION

Root growth and shoot growth are closely interrelated. Physiological regulation mechanisms of an unknown nature provide for a balanced root-to-shoot ratio adapted to the ecological conditions. Probably hormonal mechanisms which determine correlative food distribution are of great importance. There exist some generally applicable reactions norms, which vary quantitatively from species to species. The root as a heterotrophic organ is dependent on the shoot for a supply of carbohydrate and some vitamins. This can be demonstrated with cultures of isolated roots (Slankis, 1949; Seeliger, 1956, 1959; Ulrich, 1962). The level of food and auxin supply from the shoot to the root depends on the conditions affecting photosynthesis, on leaf age and leaf area, and on the utilization of photosynthate within the shoot. When the latter is low—for example, in rooted leaves—a large root system is built up very soon. The reaction of root growth to changes in rate of photosynthesis and respiration is, therefore, understandable (Richardson, 1953a,b; see also above).

Although roots are not dependent on auxin supply from shoots, hormone production of shoots seems to influence root development in a specific manner. According to Richardson (1958) defoliation inhibits length growth of roots but not root-sucker formation. Defoliation of the leading shoot bud inhibits formation of new roots, whereas roots already present go on growing.  $\beta$ -Indoleacetic acid can counteract the effect of decapitation. Probably still other hormones participate in the regulation of root growth (Romberger, 1963).

Environmental factors and cultural practices can shift the root-to-shoot ratio by incompletely known mechanisms. Soil dryness, mineral salt deficiency (especially of nitrogen), and higher soil temperatures cause an increase in ratio, whereas shading, nitrogen fertilization, higher air temperatures, and sufficient soil moisture induce a decrease in the root-to-shoot ratio. Pruning, crown cutting, and defoliation act like shading and inhibit the development of the root systems (Chandler, 1923; Heinicke, 1936; Sawage and Cowart, 1942; Wood, 1939; Hoffmann, 1966c).

Mowing and grazing of herbaceous plants decreases their root formation and the ability of their roots to compete (Weaver and Darland, 1949; Köhnlein and Vetter, 1953). Development of the root system may also be reduced by heavy fruiting. Chandler (1923) found a 50% decrease in the root system of *Prunus* after a heavy crop, and, according to Nutman (1933), *Coffea arabica* can be injured or killed by high harvests because of the insufficient supply of carbohydrates to the root system.

Some data indicate that typical species-to-species differences exist in the root-to-shoot ratio. This has been investigated mostly in young trees (see Table VI).

According to Lobanow (1960), the ratio of root surface to leaf surface is less than 1 in strongly mycotrophic trees (such as *Pinus*, *Picea*, *Larix*), whereas nonmycotrophic species reach much higher values. A value of 139 has been reported for rye (Dittmer, 1937). Mycorrhizae probably influence the root-to-shoot ratio by providing additional absorbing organs.

In older trees it is assumed that about 20% of the total weight is roots (Rogers and Vyvyan, 1934; Ehwald, 1957; Assmann, 1961). According to Bray (1963) and Whittaker *et al.* (1963), root-to-shoot ratios decrease with increasing age of trees. The above-ground and subterranean development of a tree are always in close correlation. The more exactly the real assimilation efficiency and the root quantity are ascertained, the better can this correlation be determined. The crown radius, for example, gives a lower correlation than the crown mantle area (Melzer, 1962a).

The root-to-shoot ratio changes during the growing season because of the somewhat independent development of roots and shoots. This is evident in Fig. 8. Trees having a *Quercus* type of growth flush show this most distinctly. A typical course for *Picea glauca* (Mullin, 1963) is shown in Fig. 20.

Finally we want to mention some peculiarities. According to Lemke (1955), clear correlations exist in *Quercus borealis* var. *maxima* between crown size and trunk diameter on the one hand and the mean root depth and range of horizontal roots on the other. Large crowned trees have a denser root systems than others. In contrast to other trees, the horizontal roots of *Pseudotsuga taxifolia* reportedly do not reach beyond the crown projection area (Wagenknecht, 1958), which is important from the silvicultural viewpoint. In this same species a one-sided crown development is associated with a one-sided formation of the root system.

The management of stands and trees for good crown formation is a possible way to assure the production of large, deep-reaching root systems which give a sure protection against windthrow (Wagenknecht and Belitz, 1959). Whereas in general dominant trees develop a deeper root system than suppressed ones, in *Fagus sylvatica* root depth is quite independent of the socio-ecological position of the tree (Wagenknecht, 1960).

It is interesting that the formation of a new leading shoot from a flat-topped crown in *Pinus silvestris* is correlated with the regeneration of a new taproot (Albert, 1907; Wagenknecht, 1960). According to

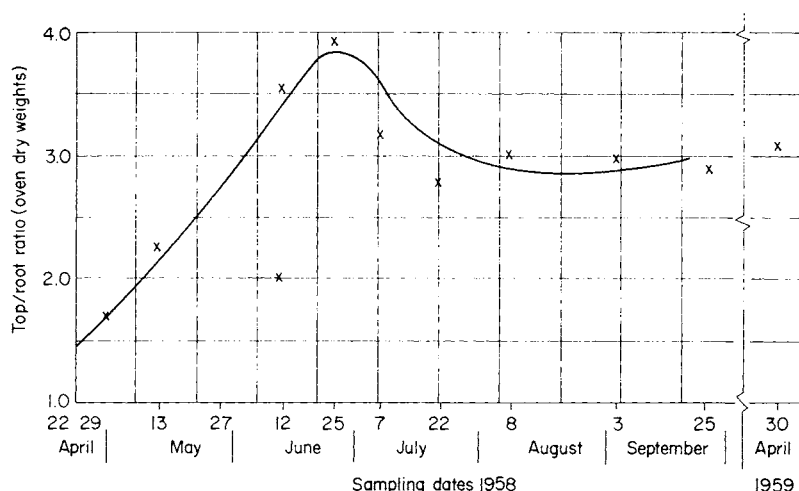


FIG. 20. Changes in the shoot-to-root ratios of white spruce *Picea glauca* seedlings during the third growing season. Based on average ratios obtained from oven-dry weights of 30 to 50 seedlings on each date (after Mullin, 1963).

Römer and Hilkenbäumer (1936, 1937) scions also have a specific influence on growth rate and branching of roots of orchard trees. Similar observations were made by Kemmer (1964).

#### D. Practical Considerations

In efforts to increase output of forest products by application of a highly developed forest science, there is a need for exact knowledge of the causal connections between environmental effective factors and tree response. In silvicultural decisions, knowledge of root growth and the factors influencing it should play a more important role than it has in the past.

It is possible, by numerous practical steps, to influence root growth and development of the root system in order to increase tree growth and to protect forests against harmful biotic and abiotic agents. There are data indicating that it is likewise possible by breeding to select clones or populations of trees which have the desired qualities with respect to root formation and root activity.

Some management measures based on knowledge of root behavior are already being applied in the forest. It is well known, for instance, that crown-tending diminishes the danger of windthrow on wet or shallow soils where trees have a tendency to form superficial root systems.

There is a fund of practical experience concerning the suitability of various tree species for heavy, difficulty penetrable soils, such as pseudogleys. On such soils, as well as on periodically flooded sites, a high root activity and a low demand for exogenous oxygen are decisive factors in determining site tolerance of a tree species.

Tree species in mixtures that have proved to be highly productive are often complementary to one another in the utilization of the site by the root system as well as in utilization of light. Therefore mixed stands often are more productive than pure stands (Erteld, 1953). New mixtures and mixture ratios can be developed theoretically from the knowledge of the general physiology of the trees and of the behavior of their root systems. This is very important in the tropics, where root competition is often a dominating factor.

Soil temperature has often been left out of consideration as a site factor, although it has been demonstrated in several instances that an increase of soil temperature brings an increase of yield. The failure of some trees on cold soils is caused by an insufficient root metabolism which causes deleterious effects because of an inadequate supply of water, mineral salts, and essential organic compounds to the shoot. The periodicity of root and shoot growth as well as the varying ability to regenerate roots during the vegetation period should be considered in the choice of planting times and times of tending and fertilizing young plantations.

Preparation of the soil should be done in such a manner that sufficient aeration is guaranteed and a deep-reaching, drought-resistant root system is formed. This may be achieved on some soils by a suitable layering of the humus by plowing.

Fertilization should be done in such a way that a harmonious root-to-shoot ratio is maintained. This is important in nurseries to minimize losses arising from climatic anomalies. Development of a shallow root system as a consequence of fertilization should be counterbalanced by other measures specifically intended to promote deep rooting.

Light conditions in stands can be influenced so that strong root systems are developed which have a high ability for competition and for utilization of deeply situated water and mineral salt sources. Here differences between tree species should be observed and considered in selecting species combinations in mixed stands.

Many failures of cultural techniques as well as growth stagnation of trees and stands have their cause in poor root growth or in damages to the root system. Their early recognition and amelioration are important

factors for increasing production. The rate of regeneration of the root system, which can be favored by several practical measures, often determines the duration and severity of growth interruptions and losses of increment.

Further examples of possibilities of increasing wood production by practical application of knowledge about root growth and root behavior could be given. At present, unfortunately, detailed data on quantitative differences in the behavior of tree species and their provenances are still lacking. Available observations are too sporadic to permit valid conclusions to be drawn from them. Therefore, reviewing the literature and summarizing the facts and opinions found therein is not easy. But in our endeavors we should not shrink from attempting to analyze the complicated physiological processes of interaction with the environment and from striving to build up a theoretical base for a high silvicultural production.

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